Early Journal Content on JSTOR, Free to Anyone in the World

This article is one of nearly 500,000 scholarly works digitized and made freely available to everyone in the world by JSTOR.

Known as the Early Journal Content, this set of works include research articles, news, letters, and other writings published in more than 200 of the oldest leading academic journals. The works date from the mid-seventeenth to the early twentieth centuries.

We encourage people to read and share the Early Journal Content openly and to tell others that this resource exists. People may post this content online or redistribute in any way for non-commercial purposes.

Read more about Early Journal Content at http://about.jstor.org/participate-jstor/individuals/early-journal-content.

JSTOR is a digital library of academic journals, books, and primary source objects. JSTOR helps people discover, use, and build upon a wide range of content through a powerful research and teaching platform, and preserves this content for future generations. JSTOR is part of ITHAKA, a not-for-profit organization that also includes Ithaka S+R and Portico. For more information about JSTOR, please contact support@jstor.org.

POSSIBLE EFFECT OF SEASONAL AND LABORATORY CONDITIONS ON THE BEHAVIOR OF THE COPEPOD ACARTIA TONSA, AND THE BEARING OF THIS ON THE QUESTION OF DIURNAL MIGRATION

CALVIN O. ESTERLY

Occidental College, Los Angeles, Calif.

There are reported here some new facts regarding the behavior of a species of marine copepod, *Acartia tonsa*. The writer has previously discussed the behavior of this organism in papers that deal with the possible relation of reactions to the habit of diurnal migration (Esterly, 1917*a*, 1919), the observations for which were made at La Jolla during the summer and fall of 1916; the animals were obtained either at the surface during the night or in deep water during the day. Such surface animals are positively phototropic when observed the next day, and are negatively geotropic in the light and positively geotropic in the dark. The specimens from deep water are negatively phototropic and positively geotropic in light and in darkness soon after they have been brought into the laboratory. The reactions of animals from the surface were noted only after the specimens had been in the laboratory for several hours because they were not to be obtained at the surface during the day and so the collecting was done at night. The possibility surely exists, therefore, that the behavior shown by animals hours after their capture may have been different in significant respects from that which would have appeared soon after their removal from the sea.

This possibility is made almost a certainty by observations obtained during the summer of 1919, when *Acartia tonsa* was taken in fairly large numbers in the morning and afternoon. The collecting was done by means of an open plankton net with a bottle tied into the peak. The specimens were taken to the laboratory right away and observations were begun at once.

When a collection is put into a dish standing before a window some of the animals are soon to be found on the side away from the window while a larger number are found on the side toward the window. The animals that I worked with during 1916 did not show that kind of distribution, at least not at the time that I used them; all were to be found on the window side of the aquarium. All or nearly all of the animals in the 1919 collections finally gathered on the side toward the light if the dish was left in front of the window for several hours, though at first there were the two well-defined portions.

As might be expected, the animals from the window side do not react to light as do those from the room side of the stock dish. The former swim toward the light while the latter swim away from the light. A shallow circular dish 16 cm. in diameter was used in a dark room to which daylight was admitted through a window 50 by 40 cm. A circle drawn on the bottom of the dish near the edge was marked off into divisions of about 15° each. The dish was placed so that one diameter was perpendicular to the window, the end nearer the window being called 90°, the opposite one 270°. The diameter parallel to the plane of the window was called 0°–180°. The center of the dish was set one meter from the window pane and animals were released one at a time from a pipette held over the middle point of the dish. When an *Acartia tonsa* swims it usually moves in a direct line without wandering around; this makes it possible to note the path taken by means of the degree marks on the circle near the edge of the dish. If an animal crossed the circle at 90° it means that it swam toward the light directly, while crossing at 270° indicates that it moved directly away from the light.

The following are examples of the behavior of specimens under the conditions mentioned above. Ten specimens from the window side of the stock dish were each tested once and they crossed the circle at these points: 35°, 100°, 90°, 105°, 45°, 85°, 90°, 90°, 90°, 75°. The paths of the first and fifth individuals diverged a good deal from a direct course toward the light, but the other animals swam toward the window. Ten other specimens in the same collection but taken from the room side of the dish crossed at: 150°, 75°, 275°, 50°, 50°, 100°, 275°, 275°, 265°, 280°. Four were positive and six were negative to the light from the window. On another day and with animals from another collection ten animals from the window side of the stock dish crossed the circle as follows: 90°, 90°, 90°, 90°, 215°, 90°, 90°, 90°, 90°, 90°—all but one moved toward the light; ten animals from the room side of the dish crossed at 270°, 225°, 270°, 75°, 90°, 270°, 260°, 260°, 275°, 270°—two moved toward the light and eight away from it. Ten specimens from the window side in a third collection crossed at 90°, 90°, 90°, 90°, 75°, 75°, 80°, 80°, 105°, 90°, 90°, all being positive. Seven individuals in a fourth collection and taken from the room side crossed at 320°, 315°, 285°, 270°, 330°, 260°, 300°—all were negative; fourteen specimens from the same collection from the window side were predominantly positive as shown by the points at which they crossed the circle: 285°, 220°, 75°, 105°, 105°, 105°, 120°, 220°, 270°, 120°, 90°, 90°, 100°, 70°.

In view of the data given above there is good reason for considering the animals that gather on the side toward the window as positively phototropic, while those on the opposite side are negative.

The conclusion from their behavior toward light that the *Acartiae* in a collection are of two sorts is strengthened by the behavior in a vertical container. For these observations the animals were put into flat bottom glass

TABLE I. *Geotropism of Acartia tonsa obtained at surface during the day. Distribution in diffuse light and darkness, given in A and B for successive hours of observation. Temperatures over 18° C. "R" means that the animals came from the room side of the stock dish; "W" means that they came from the window side. The former are negatively, the latter positively phototropic.*

Hour after capture	Whole no. of animals observed	Percentage distribution in the sections					No. of observations			Center of distr
		Top V	IV	III	II	Bot. I	Total	% showing more ans. in		
								Upper $\frac{2}{5}$	Lower $\frac{2}{5}$	
A. In the light										
R 1	488	7	4	5	6	78	81	4	95	1.5
W 1	532	69	5	3	3	20	82	81	17	4
R 2	356	25	9	5	6	55	19	28	69	2.5
W 2	393	78	4	2	4	12	70	93	6	4.3
R 3	89	36	6	4	9	45	16	44	44	2.8
W 3	166	86	5	1	—	8	30	90	3	4.6
R 4	159	44	8	3	9	36	26	54	42	3.1
W 4	52	94	—	2	—	4	11	91	—	4.8
R 5	289	47	8	7	6	32	55	56	35	3.2
W 5	318	87	4	2	1	6	63	95	5	4.7
R 6	189	61	9	4	5	21	36	72	19	3.8
W 6	240	84	6	3	2	5	48	94	7	4.6
R 7, 8	199	63	5	2	3	27	38	63	37	3.7
W 7, 8	85	76	13	2	3	6	17	100	—	4.5
R 9, 10, 11	94	58	5	3	10	24	16	56	31	3.6
W 9, 10, 11	72	82	4	–	—	14	15	93	—	4.3
B. In darkness										
R 1	329	9	7	5	3	76	65	5	89	1.9
W 1	519	46	9	4	4	37	99	54	38	3.2
R 2	186	12	9	7	1	71	38	21	76	1.9
W 2	349	46	8	4	5	37	69	49	46	2.6
R 3	57	25	16	–	5	54	11	36	45	2.5
W 3	165	68	7	2	1	22	32	88	12	4
R 4	105	30	17	9	15	29	22	36	36	3
W 4	43	58	7	5	7	23	9	78	22	3.7
R 5	240	48	12	6	2	32	47	62	21	3.4
W 5	278	64	6	5	4	21	54	85	11	3.8
R 6	173	45	11	4	6	34	35	54	31	3.1
W 6	222	57	9	6	6	22	46	72	11	3.7
R 7, 8	127	42	15	8	1	34	24	44	17	3.2
W 7, 8	75	72	8	3	5	12	13	87	12	4.2
R 9, 10, 11	67	54	13	6	5	22	10	70	—	3.7
W 9, 10	50	66	8	8	2	16	11	100	—	4
AFTER RETENTION OVERNIGHT IN THE LABORATORY										
C. In the light										
R 18–30	620	73	7	5	4	11	130	87	3	4.3
W 18–30	407	66	8	2	3	21	87	80	19	4
D. In darkness										
R 18–30	665	52	9	7	6	26	139	70	17	3.6
W 18–30	395	57	5	3	2	33	87	61	29	3.5

tubes 50 by 3 cm. The tubes were filled with clean sea water brought from off shore in glass jars. Five or six animals were put into a tube as soon as possible after the collection was obtained. The tubes were marked off into five sections of equal heights and the number of animals in each of the sections was noted from time to time. The distribution of animals from the two sides of the stock dish was compared both in darkness and in diffuse light. Usually a set of each sort was observed in diffuse light at the same time that similar sets were kept in darkness, so that the distribution in four tubes was noted at once. Most of the individuals were adult females but the behavior of the sexes is the same, so far as my observations go.

The accompanying table is arranged to show in summary the distribution of many sets of animals. The abundance in the different sections changes as the experiment is continued and the records are shown as they were taken hour by hour. In explanation of the terms used in the table it should be stated that "whole number of animals observed" is the sum of all the records of distribution in all the experiments within a given time and under given conditions. Each living animal was counted as many times as there were observations during any experiment. "Percentage distribution" is the proportion of the total number of animals observed in each section, for all experiments, to the whole number observed. "Number of observations" means the number of times the distribution was recorded. The "center of distribution" is the average position (as between top and bottom) of the whole number of animals. It is obtained by multiplying the total number of animals observed in each section by the number of the section, and dividing the sum of the products by the "whole number of animals observed." The centers are set down in units and tenths; the unit is considered to be the middle point of the section having the corresponding number. If one center is compared with another the difference between them, if any, is the magnitude of the shift of the whole population.

The difference in the behavior of animals from the window and room sides of an aquarium is plainly evident from the results given in the table. Through ten or eleven hours of continuous observation following the taking of the animals, when records were made several times an hour, there are noteworthy differences in distribution. When kept in diffuse light the positively phototropic animals (those from the window side) remain in the upper sections of the vertical tube (see the lines designated by "*W*" in part *A* of the table). Under the same conditions the negatively phototropic animals (from the room side) remain at lower levels though there is an ascent amounting to two sections of the tube during the first four or five hours (see lines designated by "*R*" in part *A* of the table).

The geotropism of negatively phototropic animals in darkness (part *B*) is practically the same as in the light: most of them when first put into the tube descend into the bottom section and ascend later. The center of distribution is in the second section from the bottom during the third hour and from that time on it is in the middle section (see the lines designated by "*R*" in part *B*). The positively phototropic animals (those from the window side) are found at higher levels than the others, as is shown by comparing the percentages and centers of "*R*" and "*W*" in part *B*. In that respect at least the behavior of positive animals ("*W*") in the light and in the dark is similar; although they descend farther in the dark than in the light and do not rise as high they are always at higher levels than "*R*" animals.

On the second day after they are obtained both sorts of animals are negatively geotropic, though more strongly so in the light (parts *C* and *D* of the table). There is practically no change hour by hour on the second day so that the summary of distribution is set down in parts *C* and *D*.

It is interesting to compare the data in the table above with the results obtained in 1916. The latter showed that surface animals were negatively geotropic in diffuse light and positive in the dark (Esterly, 1919, p. 20 and Table 1). It should be noted again that the animals came from the surface during the night and were left in the laboratory until the following day. In 1919, however, the animals could be taken at the surface during the day and were used immediately. Whether this difference in preliminary treatment accounts for the differences in behavior cannot be stated. But if retention in the laboratory accounts for the positive geotropism shown in the dark by the 1916 animals, it would seem that the same behavior could have been expected in 1919 also after holding the animals in the laboratory for hours. Yet this is not the case as may be seen in part *D* of the table; both sorts of animals ("*R*" and "*W*") are shown to be largely in the upper two fifths of the tube after they have been in the laboratory all night.

The animals observed in 1919 did not show the geotropic rhythm that was evident in 1916 (Esterly, 1917*a*). It was particularly desired to note that sort of behavior again, but it did not appear. The data in the table show that there is no particularly noteworthy change in the distribution either in the light or in the dark after about the fourth hour of observation; even on the second day the distribution is practically constant and about what it was beginning with the fifth hour on the first day.

The results given here, when considered in connection with those that appear in the other papers referred to, make one dubious as to how to apply them to the problem of diurnal migration. It may be well to glance at the experimental data in their relation to the behavior in nature. My papers have shown that two species of *Acartia* are negatively geotropic in diffuse light but positive in the dark (Esterly, 1917*a*; 1919, p. 20) when the specimens come from the surface, and that there is a rhythm in geotropism when the animals are kept in the dark that seems to duplicate on a small scale the vertical migration in the sea. The possible bearing of these results on the diurnal migration was discussed in another place (Esterly, 1919, p. 22) and it was stated that "the experiments do not show why animals obtained at the surface should not be found there during the day; indeed the laboratory results show that the species 'ought' to be at the surface during the day." The preceding statements make a brief summary of the results obtained in 1916.

In 1919, however, specimens of *Acartia tonsa* were abundant at the surface during the day and, as shown in this account of the experiments, some of the animals in a collection are positively phototropic and negatively geotropic from the first in diffuse light and (to a less extent) in the dark; while others, negatively phototropic, are at first positively geotropic in diffuse light and in darkness but later become negative.

Such discrepancies raise questions, and the first one that comes up is, What is the reason for the differences in behavior in 1919 as compared with 1916? Two answers may be suggested. It is possible that the two seasons differed to such a degree that the behavior in the sea as well as in the laboratory was altered. Whether there is anything in this suggestion or not can be ascertained, I believe, by a study of the field data obtained in 1916 and 1919 relating to the actual collections and also to the conditions of temperature, salinity and the like. The other possibility is that keeping the animals in the laboratory before beginning observation may account for the results obtained in 1916. I worked at that time on the assumption that retention in the laboratory "does not affect the behavior of animals that were obtained at the surface during the night" (Esterly, 1919, p. 18). But since the behavior of at least some of the animals taken at the surface during the day changes in a few hours the same would probably be true of animals obtained at night.

Another question that is important in this general connection is, Shall an observer apply to a problem in natural history only those experimental results obtained soon after the animals are taken from their natural surroundings, or is it desirable to wait until they have "become accustomed" to laboratory conditions? From one point of view it would seem to be better to use the results gained before the artificial conditions of the laboratory have affected the organisms any longer than necessary. On the other hand if the behavior immediately after capture differs from that shown later it may be for the reason that the animals were upset, so to speak, by removal from the sea, necessary handling and so on, and that they should have time to "settle down." It does not seem wise to attempt to fix any rule but it is plain that a student of behavior who desires to apply his results toward an interpretation of habits in nature should always look for a possible effect of laboratory conditions or something connected with laboratory procedure in modifying reactions. A more extended discussion of this matter has been given in another place (Esterly, 1919, p. 66).

If all the animals in a collecting bottle were negatively geotropic it would be comparatively easy to account for the presence of *Acartia* at the surface of the sea during the day. Some of the specimens are negatively geotropic and if this reaction takes place in the sea the organisms would be found at the surface in the light. But there are also numbers of animals whose vertical distribution in a tube does not correspond for several hours with their distribution in the sea when they were swept into the net. These representatives of the species cannot be disregarded simply because their laboratory reactions do not "fit" their behavior in nature. These specimens are as truly *Acartia tonsa* as those which are negatively geotropic from the first. If one happened to be observing animals that came from the room side of a stock dish the conclusion would be justified that *tonsa* is not found at the surface during the day.

In view of what has been said it seems proper to inquire whether the geotropism of *Acartia tonsa* as a species is to be called positive or negative. If based on experimental data the answer depends on the particular individuals observed, if the vertical distribution is noted as soon as possible after the collection is obtained. If the answer is based on the fact that specimens can be taken at the surface during the middle of a sunny day it could be said that the species is negatively geotropic. Yet the animals separate into two behavior classes in the laboratory, one being positive to horizontal light and remaining near the top of a column of water, the other being negative to light and at first positively geotropic. Because some specimens in the laboratory are negatively geotropic may it be assumed that the species at large has the same behavior? If such an assumption is made what shall be said about the positive geotropism of the other specimens that were obtained at the same time as those that remain at the top of a vertical tube? Such questions are difficult or impossible to answer at the present time, but it is important to call attention to them even if nothing else is done.

There has been much insistence in publications that deal with certain phases of the program of the Scripps Institution on the need of both experimental and field data for the solution of questions in natural history (Esterly, 1917*a*, 1917*b*, 1919; Michael, 1916). There is no need to go over this matter again here, but it is well to point out that the laboratory observations reported in this paper show facts about *Acartia* that field observations would not reveal. The plankton net could not sort the specimens that enter it into the two well marked behavior classes that appear in the laboratory. On the other hand it cannot be stated how the experimental facts are related to the vertical movement that appears to take place in the sea. The chief object in presenting the matters that have been discussed is to call attention to some considerations that must be kept in mind when it is desired to determine the relations between responses in the laboratory and habits in nature. There is no thought of suggesting that what is true of *Acartia* is necessarily true of other plankton forms, but it is likely that similar conditions will be found in other cases. At least it may be said that it is an open question how far reactions under experiment will reveal the reasons for behavior in nature, until the effect of laboratory conditions as such has been ascertained.

Summary

1. Experiments made in 1916 with specimens of *Acartia tonsa* that were taken at night at the surface and left in the laboratory for several hours showed that all the animals were positively phototropic, negatively geotropic in the light and positively geotropic in the dark.

2. In 1919 it was possible to get specimens at the surface during the day and to observe their behavior within a few minutes. Some animals are positively and some negatively phototropic. The former have marked negative geotropism in the light; in the dark also they are negatively geotropic but to a less degree. The negatively phototropic animals at first show a pronounced positive geotropism which changes after three or four hours to a rather weak negative geotropism. Both sorts of animals continue to be negatively geotropic on the second day in light and in darkness, but the reaction is more pronounced in the light.

3. It is suggested that the differences noted in the two years (1916 and 1919) may be due to oceanic conditions or to alteration in the form of response during the time that the animals are kept in the laboratory. Whatever the explanation, the application of the experimental results to the diurnal migration problem is rendered difficult and uncertain.

LITERATURE CITED

Esterly, C. O.

'17*a* The Occurrence of a Rhythm in the Geotropism of Two Species of Plankton Copepods when Certain Recurring External Conditions are Absent. Univ. Calif. Publ. Zool., 16, 393-400.

'17*b* Field Research and Laboratory Experiment: their Places in Ascertaining and Explaining Habits in Nature. Bull. Scripps Inst., no. 4, pp. 1–15.

'19 Reactions of Various Plankton Animals with Reference to their Diurnal Migrations. Univ. Calif. Publ. Zool., 19, 1–83.

Michael, E. L.

'16 Dependence of Marine Biology upon Hydrography and Necessity of Quantitative Biological Research. Ibid., 15, i–xxiii.

[*Note.*—The problem of the influence of laboratory conditions on plants and animals is becoming more and more pressing with the increasing need for exact experimentation. Although the problem may be more urgent in the case of animals than plants, still it applies to plants. For example a plant which has been grown in a greenhouse may be made to wilt, even when its roots are amply supplied with water, if placed in the open sunlight. This phenomenon is probably at the bottom of much confusion in the study of the wilting coefficient of soils. It is hoped that Professor Esterly's paper will stimulate further research along these important lines. Editor.]